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THE PINEAL AND PHOTOPERIODISM IN ARCTIC SPECIES

by
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A chapter in the book:
The Pineal Gland and Reproduction

Chapter: The Pineal and Photoperiodism in Arctic Species

Contents

The Meteorology of Polar Regions

A Comparison with Temperate Zones

Three Kinds of Bird Pineal Glands

Arctic Mammals and Photoperiod

Outline of Arctic Reproductive Physiology

Arctic Pineal Physiology: Size

Arctic Pineal Physiology: Example of Lemmings

Arctic Pineal Physiology: Broad Distribution of Species

The Pineal and Hibernation

The Pineal and Cold Exposure

Summary

The Pineal and Photoperiodism in Arctic Species

This chapter will describe the seasonal cycles of daylight and temperature in polar regions, will outline the reproductive cycles of arctic birds and mammals, and will review what is known about pineal physiology of these species.

The Meteorology of Polar Regions

We must consider the pineal of higher vertebrates in the Arctic in the context of their geographical distribution and the extreme seasonal changes found there. Both of the polar regions represent a hostile and highly variable physical environment. Although our attention will focus on the Arctic, still it should be mentioned that the birds and mammals of the South Pole region must adapt to an environment which is just as severe as the one at the tip of the North American continent and on the islands of the Canadian Archipelago. We will contrast the environment experienced by the cottontail rabbit at 30°N and the arctic hare at 72°N. Throughout the year this cottontail experiences a gradual variation in total hours of daylight only from approximately ten hours per day in winter to fourteen hours in summer. On the other hand, there are 29 species of land mammals which at 72°N each year experience 82 days of continuous lack of sunlight followed by a rapid change up to the first of May when a period of 82 days of continuous sun above the horizon begins.

During the period of rapid change, the day lengths increase by as much as 27 minutes per day (Fig. 1). The characteristic of the light change in the temperate zones is that of a small, slow, regular change each day while at 72°N in the Arctic it is feast or famine; there is relative constancy with very reduced daylight for the long period of three months followed by rapid changes, then constancy for another long period of time except for the variation of cloudy days. Surely any organs which transduce photoperiodic signals must be designed differently in the temperate zone and in the Arctic. In addition to demanding photoperiodic changes, there are other meteorological changes each day which are so irregular that they cannot serve as a zeitgeber for circadian physiological rhythms. For example, we have reported the daily changes in light, barometric pressure, and air temperature (6) for the spring period of continuous daylight; the only regular clue found is the distance of the sun from the horizon in the north (7).

In the winter the air temperatures are extreme so that annual range is greater than 55°C along the coast. Relative humidity values are extremely low in the winter and rather high in the summer. In winter, wind chill effects must be taken into account in studying the biology of a mammalian species residing there; on the coast the combination of 25 miles per hour and -30°C is not uncommon providing an equivalent temperature of -65°C. Near Prudhoe Bay an equivalent

temperature of -100°C again is not uncommon. The impact of such an environment on arctic birds and mammals may be partially reflected in their pineal physiology. Because this gland is not only associated with photoperiodic responses with some species, but also with resistance to cold (14; 21) , it seems particularly appropriate to study the pineal in these animals. What may be a small contribution by this gland on temperate zone animals may be amplified in arctic species.

A Comparison With Temperate Zones

Most of the studies on pineal glands have been made on domestic temperate zone animals. Nevertheless, the principles found in these studies are those which must in the future be applied to arctic animals. All temperate zone higher vertebrates are not photoperiodic and it would seem that this might be even more the case in arctic animals. Contrarywise, even when an animal does depend on day length to control annual reproduction, the pineal gland is not necessarily involved with this control, but it usually is (5). We must now examine some specific cases of these principles and attempt to apply them to arctic animals.

Three Kinds of Bird Pineal Glands

To emphasize the independence of some birds from photoperiodism, the sooty tern is a good example; according to MARSHALL (13) this bird lives in a fairly even climate and

reproduces every nine months. Since it is clearly independent of photoperiodism, then the pineal gland of this species must have other assignments than to act as transducer of annual light signals. MARSHALL gives numerous other examples. A similar situation must be the case with African finches kept in captivity by Emil WITSCHI (27) ; these did not need a photoperiodic signal to change their plumage on schedule each year when kept under constant conditions. Once again, if the pineal gland had an assignment, it would be primarily to control the day-night rhythm; the daily pineal secretion rhythm is known to persist (21). It is not only unusual birds like the last two but a few common year-round residents such as the blue jay which are not photoperiodic (1). The point is that it is reasonable to look for non-photoperiodic animals in the Arctic regions.

In contrast, consider photoperiodic effects on arctic bird migrants such as the golden plover. Other types of birds, if they are resident in the winter in Texas, are able to use a photoperiodic signal. As days begin to lengthen, the migratory urge and reproductive organs may develop under the stimulus of day length. The golden plover, on the other hand, leaves the pampas of Argentina to migrate across the Equator thus experiencing no regular photoperiodic change; they are migrating north at about the time when all parts of North America are having a 12-hour day simultaneously. So far the bird has not received a systematic periodic signal. As the

bird arrives in the north, it begins nesting, again without the usual types of photoperiodic changes because continuous light is now present. It is as if the bird has left a 12-hour photoperiod and very soon "bursts into" a period of continuous light.

There is no regular diminution of the continuous light near midnight in the Arctic because frequently there are many cloudy mornings and clear evenings so that light intensity is often greater in the evening than in the morning (6). It is evident that many of the arctic birds (all of which are migratory) experience a complexity of photoperiodic signals compared to temperate zone birds. The environmental signals are further complicated because most migratory birds are apt to fly at night but upon arriving at the nesting grounds they become day active. This is not always the case. There are two common species of owls nesting in the Arctic (snowy and short-eared); the short-eared owl appears to be day-active throughout its entire life while the other one is nocturnal except when it nests in the continuous light of the Arctic. The biology of the two birds is rather different because the short-eared owl nests south to central United States as well as in the Arctic.

There is one photoperiodic pattern which could drive arctic birds to migrate south; that is the decrease in daylight in August. A study of the pineal glands of the short-eared owl and the golden plover in winter and in summer would be fruitful.

Arctic Mammals and Photoperiod

It is difficult to find a spring photoperiodic pattern associated with migrating birds in the Arctic but the picture is rather different with mammals. The 29 species of mammals in the Arctic are migratory only to a minor extent. Alaskan arctic caribou migrate easterly or westerly and not north and south (2, p. 243). Thus arctic mammals appear to experience continuous light during their reproductive period more than any other animal. Some of them have a restricted breeding time such as the caribou and the musk ox, while others such as the lemming actually breed in both winter and summer (15). To complicate matters, there are numerous kinds of weasels in the Arctic which are known to have delayed implantation (2); their photoperiodic responses would be quite different from mammals that respond to an increase in day length. All of these mammals experience a period during February and March when there is a changing photoperiod after several months of unchanging continuous darkness, except for occasional dim light. From April on, a strong photoperiod signal is lacking; relative constancy begins and this condition lasts until August. Thus for arctic mammals the photoperiodic system is more one of relative constancy than of regular daily contrasting variation as found in the temperate zone. The continuous light is a normal function of Arctic living; this is not the case with temperate zone animals such as the white rat. It

has been well established that continuous light is a stress for the laboratory rat (19, p. 158; 22). Yet the principles of the influence of continuous light upon the pineal gland have been obtained almost entirely from this species (5).

Thus we must predict that in the normal continuous light of the Arctic, rodent pineal physiology will be different from that in the white rat.

Outline of Arctic Reproductive Physiology

The mammals under discussion have regular reproductive seasons relative to the season of continuous light. Details are presented in Table I. It is necessary to provide two descriptions for lemmings because of their remarkable periodic fluctuations in population. Approximately every four years fluctuations occur to such an extent that only two lemmings may be found per acre compared to 400 in a year of peak populations. Thus there may be two separate pineal "histories" for lemmings to be studied, one when the population is "low" and unstressed, the other when it is in a stressful state of high population. There is little to be said directly about the pineal gland of arctic mammals except that this organ regulates the molt and reproduction of weasels (24). There will be further discussion later of the pineal glands of some of the birds and sea mammals, and especially of lemmings.

Another aspect of reproductive physiology is the photoperiodic signal in some cases known to act through the pineal and perhaps through changes in the nightly "pulse" of melatonin (21). Consider once again the constantly adjusting day-night rhythms of birds flying north to nest in the Arctic. In this case the evidence is against a contribution from the pineal gland; QUAY (18) implies that there is a faster adjustment of animals which are having the light cycle changed each day by those animals which have been pinealectomized. In this context the pineal would be considered a protective or stabilizing organ rather than one designed to assist rapid readjustments when day length is changing.

Arctic Pineal Physiology: Size

The most definitive work on variation in size of the pineal gland has been presented by RALPH (20) who has related size variations to geography. In cautious terms, he suggests that animals which tend to inhabit the tropical regions are more apt to have no pineal body or a small one, while large pineal glands are more apt to be found at high latitudes. In another aspect of this hypothesis he suggests that there could also be some relationship to whether a species is nocturnal. He points out that owls have the greatest variation among birds in respect to pineal size and those with the largest pineals are the most diurnal. It is significant that the two owls which nest in the Arctic are diurnal.

and REITER (23)
RALPH also point out that the pineal of the king penguin is very large. The largest pineal in his survey is found in the northern fur seal, Weddell seal, sea lion, walrus, and harbor seal. The suggestion that arctic mammals have large pineal glands has received some support from a recent study on lemmings (10); brown lemmings in winter, animals averaging 50gm, were found to have pineal glands with approximately the dimensions of those in 200gm rats(1.22mm/50g ; 1.42mm/200g). It is appropriate at this point to discuss the meaning of a large pineal gland. In the white rat, both volume and cytological element vary with day length; experimentally the pineal weight is reduced by continuous light (5). It is not known how many species this applies to. Next, does the pineal vary in size from day to night? According to FISKE (5) this does occur with the white rat. The parallel observation was made by RALPH (21); there is a ten-fold variation in production from day to night of melatonin in chickens and rats (2ng light; 20ng dark). This nightly persistent surge in the rat pineal is also found in the brain and serum. Constant darkness significantly dampens the serum melatonin pulse, however. Nevertheless, the point is made that secretory activity of pineals varies with size. As RALPH (20) expresses it, "large pineals have larger physiological roles." The dilemma still remains when large pineal glands are described in lemmings or other arctic species as to whether these are enlarged or permanently large.

Only by careful comparisons [illegible] day and night, pineal; and with seasonal changes can this be determined.

Arctic Pineal Physiology: Example of Lemmings

We have reviewed above some responses of temperate zone mammals under laboratory circumstances, and now must consider the reproduction of brown lemmings: animals which have a peak of breeding in summer and again in February and March. Because February is a period of nearly continuous darkness (there is dim light sometimes at noon), and because the summer breeding period is in continuous light, one would predict that this animal is not photoperiodic. One pilot experiment has been done which is evidence to the contrary: when brown lemmings (Lemmus trimucronatus) were maintained in continuous light with and without pineal glands, and in another group in continuous darkness with and without pineal glands for 30 days, the testes of the intact animals in continuous light were significantly larger than those in continuous darkness (10). This presumed influence of darkness and possibly of some pineal hormone was prevented by pinealectomy. There was no significant difference between the testes of the pinealectomized lemmings in darkness compared with the control animals and the pinealectomized animals in daylight. The exposure to artificial continuous light and continuous darkness lasted only four weeks, and this experiment should be repeated with longer exposures.

By what mechanism does continuous light act on the pineal of a rodent like the lemming? According to FISKE (5), in the white rat the effect is direct. In her experiments she eliminated an indirect effect of the pituitary, gonads, adrenals, or thyroid.

Arctic Pineal Physiology: Broad Distribution of Species

Although the evidence of hypertrophy of the pineal in arctic species is strong, we must look closely at the individual species involved. The large gland in the Weddell seal and the king penguin suggest that the great battery of changing photoperiods in polar regions may be associated with the fortuitous adaptation of an abundantly secreting pineal gland. Seals and penguins, however, are not necessarily arctic animals. One seal species is tropical, the California sea lion also occurs in the tropics, and one genera (Mirounga) occurs in both the north and south temperate zone (26). As for penguins, only two of the seventeen species reach the shores of the polar continent or even cross the Antarctic Circle (16). Five more nest in regions varying between ice-covered and ice-free; six species belong definitely to south-temperate latitudes; and four are tropical or sub-tropical. Compare the northern latitudes attained by four different species:

Galápagos Islands: Equator
Brazil: 24° to 30°S
Angola: 16°S
West Australia: about 22°S

Furthermore the hair seal (<u>Phoca vitulina</u>) which is the often-quoted example of an arctic animal with a large pineal, also occurs in the temperate zone. Two subspecies of this species occur as far south as 22°N. An exciting experiment for the future will involve measuring the pineals of southern and northern specimens in winter and summer.

The Pineal and Hibernation

The pineal and hibernation deserves mention here because three hibernators occur abundantly on land at 72°N and on the islands further north; these are <u>Marmota caligata</u>, <u>Spermophilus undulatus</u>, and the grizzly bear (2;9). The first species occurs from Point Barrow to mid-Idaho, although seven mainland subspecies are found. The <u>Spermophilus</u> (arctic ground squirrel) occurs from Point Barrow and Hudson Bay to British Columbia (five mainland subspecies are recognized). For reproductive correlation with annual photoperiod perhaps a better species would be <u>Marmota monax</u> (another hibernator) which has a range from central Alaska to the Florida border. The relationship of the pineal to hibernation was introduced by PALMER and RIEDESEL (17); when melatonin was injected into squirrels, they went into hibernation more rapidly and had longer bouts of hibernation. Similar experiments should be done on arctic hibernators.

The Pineal and Cold Exposure

The case for a protective role of the pineal in arctic

mammals is supported by the experiments of MILINE who showed that pinealectomized rats are more sensitive to cold than normal rats (14). His correlative studies of the supraoptic nucleus suggest that the pineal gland is responsible for the behavior of this structure at low temperatures. It should be pointed out that the arctic species which are the closest relatives to the rodent studied by MILINE are two species of lemmings. They are usually protected in winter in their subnivean habitat under the snow. One species (Dicrostonyx groenlandicus) is white in winter, is more cold tolerant, and does come out on the surface of the snow. The brown lemming (Lemmus trimucronatus) is less cold tolerant and remains (and breeds) under the snow. A comparison of their pineal glands will prove interesting. The white fox is another special case because it changes its coat color in the summer. Details are found in UNDERWOOD (25).

The species which cannot escape the challenge of intense arctic cold are the caribou, moose, and musk ox. Many moose, in spite of their long limbs as radiators, do survive above the Arctic Circle, and must tolerate long black nights of standing in moose-yards at -70°C, or with a wind chill very much lower. It is these animals which experience the combination of the most extreme photoperiod and the most harsh conditions of cold exposure.

Future studies of the pineal of cold-exposed animals must be framed in the context of the rule: photoperiod

alone can prepare the animal for cold, without cold exposure. The experiments supporting this rule are found in Table II. The concept is reasonable since norepinephrine is the hormone of cold exposure (8). Injections of norepinephrine simulate cold exposure and are a test for the degree of cold acclimatization. This hormone is abundantly produced in the pineal with over twice the content in the pineal of the rat in nighttime compared to daytime (3, p.31). Because of this occurrence in the pineals of control rodents, it will be reasonable in the future to do correlative studies looking for norepinephrine production in the pineals of arctic animals exposed to severe cold.

Summary

Many simple experiments on arctic animals should be done because the results may amplify small pineal effects seen in temperate zone animals, and because exposures to continuous darkness and continuous light are normal for arctic species. The initial experiments might involve simply pinealectomy and the administration of melatonin. One may look for effects upon the status of the gonads, estrus in seasonal breeders, and changes in coat color in winter.

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Table I

EXAMPLES OF ARCTIC REPRODUCTIVE CYCLES

Species	Condition	Season	Photoperiod	Breeding	Raise Young
Snowy Owl (*Nyctea scandiaca*)	When low lemming population	Summer	Constant light	None	None
Snowy Owl	When high lemming population	Summer	Constant light	Active	Up to 12 eggs per nest
Arctic Fox (*Alopex lagopus*)	Coat changes white to gray	Spring	Alternating day/night	March	---
		Summer	Constant light	---	May
Brown Lemming (*Lemmus trimucronatus*)	Low population year	Summer	Constant light	Consecutive litters	Fewer litters after mid-summer
Brown Lemming	High population year*	Summer	Constant light	More and larger litters	Population** "crash" at summer end; no young animals
Brown Lemming	Start of high population year; sometimes every year	Winter	Constant darkness and begin alternating day/night	Breed under snow in Feb. and March	Smaller litter size in winter

* Characteristics are high body weight with large litter sizes.

** Characteristics are hyperadrenalism, depletion of pituitary ACTH, elevated circulating adrenal progesterone, lowered gonadotrophic hormone, and lowered resistance to cold stress. (R.V. Andrews, personal communication, 1974).

Table II

EXAMPLES OF COLD ACCLIMATION WITHOUT COLD*

	Photoperiod	Experiment
Deermice (Ref. 12) *Peromyscus leucopus*	16:8 LD control 9:15 LD experimental Experiment done at T_A 26°C	Norepinephrine was injected (6mg/100g body wt). There were higher levels of non-shivering thermogenesis in short photoperiod mice relative to long photoperiod treatment.
White Rats (Ref. 4) *Rattus norvegius*	16:8 LD control 9:15 LD experimental Experiment done at 22°C and -38°C	Control plasma free fatty acids were much higher under short photoperiod than the long one; short photoperiod animals, under cold exposure, raised their FFA much higher than long photoperiod animals.
Goldfish (Ref. 11) *Carassius auratus*	Long daily photoperiods Short daily photoperiods T_A 26°C	Fish in long photoperiod became more resistant to heat; those maintained in short photoperiod became more resistant to chilling.

* Other examples have been obtained using deermice, hamsters, and birds.

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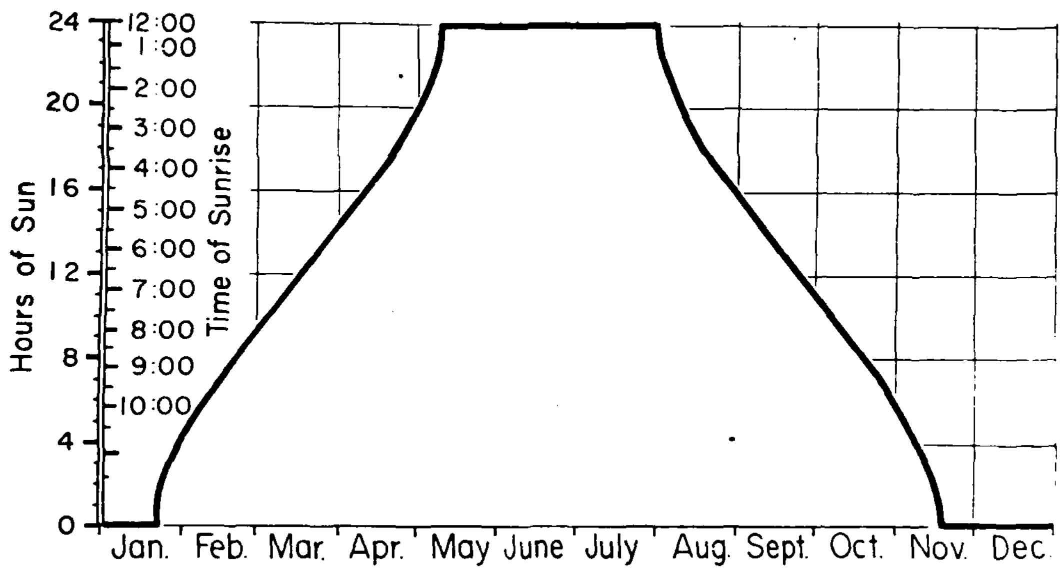
Caption

Figure 1

The annual cycle in day length at Point Barrow, Alaska, which is at latitude 71° 20N, and 1,760 kilometers from the North Pole.

Figure 1

ANNUAL HOURS-OF-SUNLIGHT AT POINT BARROW, ALASKA



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